Equipped to cope with climate change: Traits associated with range filling across European taxa

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What can life-history traits tell us about species' range-shift responses to climate change? A multi-taxon approach

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Complete List of Authors:	Estrada, Alba; Universidad de Malaga, Animal Biology Morales-Castilla, Ignacio; McGill University, Biology Meireles, Catarina; Universidade de Evora Caplat, Paul; Lund University, Centre for Environmental and Climate Research Early, Regan; University of Evora, Rui Nabeiro Biodiversity Chair
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Abstract:	In order to understand the ecological effects of climate change it is essential to forecast suitable areas for species in the future. However, species' ability to reach potentially suitable areas is also critical for species survival. These 'range-shift' abilities can be studied using life-history traits related to four range-shift stages: emigration, movement, establishment, and proliferation. Here we use the extent to which species' ranges fill the climatically suitable area available ('range filling') as a proxy for the ability of European mammals and birds to shift their ranges under climate change. We detect which traits associate most closely with range filling. Drawing comparisons with a recent analysis for plants, we ask whether the latitudinal position of species' ranges supports the assertion that post-glacial range-shift limitations cause disequilibrium between ranges and climate. We also disentangle the relationship between range size and filling. For mammals, generalists and early reproducing species have the greatest range filling. For birds, generalist species with high annual fecundity, which live longer than expected based on body size, have the greatest range filling. Although we include traits related to the four range-shift stages, only traits related to establishment and proliferation ability correspond to range filling of mammals and birds. Species with the greatest range filling are those whose range centroid falls in the latitudinal centre of Europe, suggesting that post-glacial range expansion is a leading cause of disequilibrium with climate, although other explanations are also plausible. The positive relationship between range size and filling suggests that low range filling could indicate either positive or negative outcomes for species with narrow ranges under climate change. Range filling of plants is lower than that of mammals or birds, suggesting that plants are more range-limited by non-climatic factors, and therefore might be less likely to undergo range shifts.

What can life-history traits tell us about species' range-shift responses to climate change? A multi-taxon approach

Alba Estrada*[1,2], Ignacio Morales-Castilla[3,4], Catarina Meireles[5], Paul Caplat[6] and Regan Early*[7]

1: Biogeography, Diversity and Conservation Research Team, Department of Animal Biology, University of Málaga, Spain

2: Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University – Campus Mieres, Spain

3: Department of Biology, McGill University, Montréal, QC, Canada

4: Quebec Centre for Biodiversity Science, Montréal, QC, Canada

5: CIBIO/InBIO, Universidade de Évora, Portugal

6: Centre for Environmental and Climate Research, Lund University, Sweden

7: Centre for Ecology and Conservation, University of Exeter, UK

*Corresponding authors: albaestradaa@gmail.com, r.early@exeter.ac.uk

Keywords

Life history, climate change, dispersal, persistence, range limits, range size

Abstract

In order to understand the ecological effects of climate change it is essential to forecast suitable areas for species in the future. However, species' ability to reach potentially suitable areas is also critical for species survival. These 'range-shift' abilities can be studied using life-history traits related to four range-shift stages: emigration, movement, establishment, and proliferation. Here we use the extent to which species' ranges fill the climatically suitable area available ('range filling') as a proxy for the ability of European mammals and birds to shift their ranges under climate change. We detect which traits associate most closely with range filling. Drawing comparisons with a recent analysis for plants, we ask whether the latitudinal position of species' ranges supports the assertion that post-glacial range-shift limitations cause disequilibrium between ranges and climate. We also disentangle the relationship between range size and filling. For mammals, generalists and early reproducing species have the greatest range filling. For birds, generalist species with high annual fecundity, which live longer than expected based on body size, have the greatest range filling. Although we include traits related to the four range-shift stages, only traits related to establishment and proliferation ability correspond to range filling of mammals and birds. Species with the greatest range filling are those whose range centroid falls in the latitudinal centre of Europe, suggesting that post-glacial range expansion is a leading cause of disequilibrium with climate, although other explanations are also plausible. The positive relationship between range size and filling suggests that low range filling could indicate either positive or negative outcomes for species with narrow ranges under climate change. Range filling of plants is lower than that of mammals or birds, suggesting that plants are more range-limited by non-climatic factors, and therefore might be less likely to undergo range shifts.

Introduction

Calculating the geographic areas that will be environmentally suitable for species in the future has been widely employed in recent decades to forecast changes in species' distributions (Huntley et al. 2008, Real et al. 2013, Estrada et al. 2016a) and to suggest locations for future reserve networks (Araújo et al. 2011, Alagador et al. 2014). The majority of these studies employ Species Distribution Models (SDMs) that use environmental variables to explain species distributions (Huntley et al. 2008, Araújo et al. 2011, Real et al. 2013). However, most SDM studies do not consider the ability that species may have to reach, and establish within, potentially suitable areas (Engler et al. 2012), which may be critical for species survival (Pearson et al. 2014). An effort to include range-shift ability in SDMs has recently emerged, but is limited by the scarcity of data, often leading to the use of simplistic range-shift scenarios (i.e. full movement, no movement, and partial movement to the new range) (Bateman et al. 2013). To circumvent these problems, and get a better understanding of species' capacity to maintain populations under environmental change, it is becoming increasingly common to make generalisations based on life-history traits (Estrada et al. 2016b). Life-history traits are *sensu stricto* defined as those morphological, physiological or phenological characteristics measurable at the individual level that have an effect on individual performance (Violle et al. 2007). However, measurements of environmental tolerance or habitat specialization, termed 'indicative' traits have also been used to inform range shifts (Triviño et al. 2013, Pearson et al. 2014). Indicative traits ultimately depend on life-history traits but also on behavioural and other functional traits. We therefore include indicative traits as 'predictive' life-history traits for the purpose of this paper (Estrada et al. 2016b).

Many predictive traits are relevant to species' responses to climate change. We previously proposed that traits should be selected based on their association with the four stages of the range-shift process: i) emigration, i.e., individuals embark on a journey away from their natal location, ii) movement or dispersal, i.e. the transfer of individuals or propagules away from the location in which they originated, iii) establishment of self-sustaining populations following

dispersal, and (iv) proliferation following establishment, which increases the number of dispersers and accelerates the founding of more populations (Estrada et al. 2016b). One of the problems in trait research is that traits are recorded inconsistently between species, but we suggest that this can be circumvented by grouping traits into broader categories that correspond to the range-shift stages (Table 1). Species' performance at each of the stages can be informed by predictive traits.

Recent studies have attempted to use a suite of predictive traits to identify the species that are well positioned to cope with large-scale environmental changes, in particular climate change (Foden et al. 2013, Triviño et al. 2013, Garcia et al. 2014, Pearson et al. 2014). But the choice of predictive traits is based on little or no quantitative evidence. Estrada et al. (2016b) suggested that the degree to which a species occupies the areas that are currently climatically suitable for it ('range filling') could be a proxy for species' capacity to undergo range shifts as climate changes. Species that have the lowest climatic range filling are those with the greatest degree of non-climatic range limitations. Thus the predictive traits that correlate with range filling could be used to indicate the species that will face non-climatic range shift limitations. This is particularly the case in Europe, where species ranges are thought to be strongly shaped by the ability to expand from glacial refugia, and species traits indicate this ability (Svenning and Skov 2004, Dullinger et al. 2012, Estrada et al. 2015). Some studies have previously identified traits that are related to species' geographical ranges (Bohning-Gaese et al. 2006, Munguía et al. 2008, Angert et al. 2011, Laube et al. 2013a, Laube et al. 2013b, Auer and King 2014, Bradshaw et al. 2014), but have not considered traits that correspond to the four stages of the range-shift process.

Here we examine the traits that correspond to range filling of European mammals and birds and use the four stages of the range-shift process as a framework to detect the predictive traits that would help species to cope with climate change.

A major limitation on European species' current ranges is thought to be the degree to which they have been able to expand from glacial refugia, with species living predominantly in the southern part of Europe having undergone the least expansion (Nogués-Bravo et al. 2014). If this is the case, then species living in the southern part of Europe could be the most affected by climate change because of their limited ability to range shift. Alternatively, species in southern Europe could be restricted to that region because of their climatic tolerances. The first hypothesis, of post-glacial range-shift limitation, would be supported if southern European species had a lower degree of range filling than species elsewhere (Svenning and Skov 2004). We therefore examine the relationship between range filling and the latitudinal position of species' ranges, for European mammals, birds, and plants.

Finally, it has recently been suggested that species with narrow ranges may experience greater non-climatic limitation than more widespread species (Early and Sax 2014). We therefore disentangled the relationship between range size and range filling for European mammals, birds and plants.

Material and methods

We applied a similar approach to that used in Estrada et al. (2015). We used presence data of native European mammals and breeding birds on 50 km x 50 km UTM grid cells (Hagemeijer and Blair 1997, Mitchell-Jones et al. 1999) within Europe from -10º 9' 23'' – 30º 43' 10'' E and from 34º 59' 30'' – 70º 58' 33'' N. Species present in fewer than 20 grid cells were removed from analyses to reduce errors associated with extremely narrow-ranged species, for which distribution data are unlikely to reflect climate tolerances (Stockwell and Peterson 2002, Bradley et al. 2015). The final dataset contained 335 birds and 125 mammals. Data for European plants were those used in Estrada et al. (2015).

101

102 **Geographical range characteristics**

103 We estimated range filling as the proportion of climatically suitable area, i.e., the potential
104 range, that it is occupied (Svenning and Skov 2004), following the methodology of Estrada et
105 al. (2015). To calculate the climatically suitable area we conducted a PCA for the following
106 climate variables using all grid-cells in the study region: temperature of the coldest and the
107 warmest month and annual precipitation. We used the first two axes of this PCA to construct a
108 two-dimensional climate space, on to which we plotted each species' distribution, and
109 calculated the minimum convex-hull polygon that included all of the species' occurrences. The
110 grid-cells with climatic conditions that fell inside this polygon were considered the potential
111 range, and range filling was the proportion of these grid-cells that were occupied ('range
112 filling100'). Species' occurrences in relatively extreme climatic conditions that are not
113 representative of the species' environmental tolerances would increase species' potential
114 ranges, and possibly bias our results. To test for any such effect, we also calculated potential
115 range using the minimum convex-hull polygon that encloses the 95% most environmentally
116 central species' occurrences ('range filling95'). Climatic variables were derived from the
117 climatic research unit (CRU) dataset at 10' resolution (New et al. 2002). 10' climatic variables
118 were averaged inside each 50 km x 50 km grid-cell.

119

120 **Species' predictive traits**

121 We tested the strength of the relationships between range filling and species' traits related to
122 emigration, movement, establishment, and proliferation (Table 1). The rationale and
123 hypotheses for each trait are detailed below, and further information on how each trait was

124 measured, categorised or transformed (e.g. allometric correction) is given in Appendix S1 in
125 Supplementary material. Trait data were obtained from the databases and studies recorded in
126 Appendix S1. Traits are sorted following the four stages of the range-shift process and the trait
127 categories associated with these stages (Table 1). Parentheses after the trait name indicate the
128 range-shift stage to which the trait belongs to: emigration (Em), movement (M), establishment
129 (Est), and proliferation (P). A sign after this code indicates our hypothesis of the relationship of
130 the trait with range filling: positive (+), negative (-), or either positive or negative (±). Note that
131 some predictive traits were available for only one of the groups, i.e. birds or mammals (Table
132 1).

133 - *Migratory status* (Em, M, ±): The relationship of this trait with range filling can be
134 hypothesised to be positive or negative. On the one hand, migrants tend to be better
135 dispersers (Paradis et al. 1998), which in turn increases range size (Laube et al. 2013b), but, on
136 the other hand, they have high site fidelity and may show lower range shifts than resident
137 species (Lehikoinen and Virkkala 2016, Välimäki et al. 2016).

138 - *Migration distance* (M, +): We collected migration distance for birds from Végvári et al.
139 (2010) who estimated it as the orthodrome (great circle) distance between the midpoint
140 values of longitudes and latitudes occupied in the summer and winter distributions. We
141 hypothesised a positive relationship between range filling and this trait, as long-distance
142 migrants can be considered better dispersers. Information on this trait was only available for
143 bird species.

144 - *Colonial breeding behaviour* (Em, Est, -): We used two possible values for this trait: colonial
145 for bird species nesting in clusters and territorial otherwise. Territorial species make use of the
146 territory on a larger extent than colonial species do and so we hypothesised that they will have
147 larger geographical ranges. Additionally colonial species show high site fidelity, and Allee
148 effects may mean that a certain number of conspecifics are needed to breed (Stephens et al.

149 1999), so colonial species may show lower range filling than territorial species. Information on
150 this trait was only available for bird species.

151 - *Home range* (M, +): Home range size is proportionally correlated to dispersal distance of
152 mammals when considered independently of body size (Bowman et al. 2002), so we
153 hypothesised higher range filling for species with larger home ranges. Information on this trait
154 was only available for mammals.

155 - *Group* living (Est, ±): Species living in groups usually cooperate and should have lower
156 extrinsic mortality via reduced predation risk (Stephens et al. 1999). Thus group living confers
157 advantages when establishing in new environments, so the relationship with range filling could
158 be positive. On the other hand, population growth of some species may depend on living in
159 groups and a certain group size may be needed to colonize new areas, and therefore the
160 relationship with range filling could be negative. This trait was only available for mammals, but
161 there are parallels with colonial breeding behaviour in birds.

162 - *Longevity* (Est, +): Species with longer lifespans have more opportunities to reproduce, which
163 may allow breeding to occur when conditions are more amenable. Thus longevity is thought to
164 increase persistence during unsuitable climatic conditions (Estrada et al. 2016b), easing
165 establishment and, consequently, range filling.

166 - *Sleep behaviour* and *Hide behaviour* (Est, +): Hibernation is associated with increased annual
167 survival (Turbill et al. 2011); and both sleep and hide behaviours are associated with lower
168 extinction risks (Liow et al. 2009), which could result in higher range filling. Information on
169 these traits was only available for mammals.

170 - *Annual fecundity* (Est, P, +): High annual fecundity could lead to high local abundances which
171 are often correlated with large range sizes (Laube et al. 2013b).

- *Annual productivity* (Est, P, +): High productivity corresponds to species that have many clutches throughout the year, each having a low number of individuals. We hypothesised a positive relationship of productivity with range filling, as it increases the number of breeding opportunities, increasing the probability of breeding during brief periods when conditions are amenable.

- *Body Mass* (Est, P, ±): Body mass is a key morphological characteristic of animal taxa that strongly correlates with a suite of other life-history traits. As with migration, the relationship of body mass with range filling can be hypothesised to be positive or negative. Large-bodied species have lower fecundity and slower life histories, which might lead to higher population extinction risks and reduced range size (Purvis et al. 2000, Cardillo et al. 2005, Bradshaw et al. 2014). On the other hand, well-known biogeographical patterns such as Bergmann's and Rapoport's rules, support a positive relationship between body size and range size, at least in the northern hemisphere (e.g. Morales-Castilla et al. 2012a, Morales-Castilla et al. 2012b). Further, brain size (see below) is positively correlated with body size, and it can be a key characteristic allowing species to fill more their ranges (Estrada et al. 2016b).

- *Sexual maturity age* (Est, P, -): Vertebrate species with lower age at maturity proliferate rapidly and show high fertility (Herrando-Pérez et al. 2012), thus having advantages to establish and proliferate in new environments. Consequently, we hypothesised higher range filling for these species.

- *Inter-birth interval* (Est, P, -): A longer inter-birth interval is associated with an elevated extinction risk, as species with slow life histories are less able to compensate for increased mortality through increased fecundity (Purvis et al. 2000). We hypothesised a negative relationship of this trait with range filling. Information on this trait was only available for mammals.

196 - *Habitat breadth* (Est, P, +): Habitat breadth may be positively related to range filling as more
197 habitat is available to be occupied for species that are generalists. Additionally, more habitat
198 means larger population sizes, more robustness to environmental fluctuations, and a greater
199 number of individuals that can leave the natal patch and colonise new habitat (Laube et al.
200 2013b, Estrada et al. 2015).

201 - *Diet breadth* (Est, P, +): This trait is indicative of ecological generalization. For the same
202 reasons as 'habitat breadth', species with broader diets are hypothesised to have larger ranges
203 and range filling, though the results so far are equivocal (Angert et al. 2011, Laube et al.
204 2013b).

205 - *Trophic level* (Est, P, +): We used this trait as a categorical variable with four classes:
206 herbivore, carnivore - mainly vertebrates, carnivore - mainly invertebrates, and omnivore
207 (Gregory et al. 2007). We hypothesised higher range filling for omnivorous species on the basis
208 that they could colonize new areas more easily than species restricted to a specific type of
209 food.

210 - *Brain size* (Est, P, +): Species with higher relative brain size with respect to body mass are
211 more successful at establishing themselves in new environments, as larger brains can allow
212 individuals to modify or create new behaviours (Sol et al. 2005), conferring high competitive
213 ability and therefore more capacity to colonize new areas and proliferate. So we hypothesised
214 a positive relationship with range filling.

215 - *Population density* (Est, P, +): Higher population density would mean higher capacity to
216 proliferate and expand geographical ranges (Fritz et al. 2009). Information on this trait was
217 only available for birds.

218

Modelling method

Analyses for mammals and birds were performed separately, and followed the methodology used by Estrada et al. (2015). We performed GLMs with range filling as the response variable and predictive traits as independent variables. As range filling showed over-dispersion, we fitted it with a quasi-binomial distribution. Data on each trait were not available for all species (Tables 2 and 3). Therefore, we conducted the analyses in four steps: 1) we first performed univariate models for each life-history trait, testing for linear and unimodal responses. 2) we constructed multivariate models in the following way: all variables that in the univariate models accounted for more than 10% of the explained deviance were considered to be 'core' variables. 'Candidate' explanatory variables were considered to be those that accounted for less than 10% of the explained deviance but for which $P < 0.25$ in the univariate models (Hosmer and Lemeshow 2000). We then constructed multivariate models that contained the core variables and one of the candidate variables, and repeated this for all candidate variables. Depending on the taxon analysed and on the response variable (range filling95 or range filling100), this resulted in models that contained three or four variables. 3) for each of these models we performed an information-theoretic approach to obtain Relative Variable Importance ('RVI') (Burnham and Anderson 2002). For each taxon and response variable we identified variables with RVI > 0.5 in the second step (Estrada et al. 2015). We tested all possible combinations of these variables using the function *dredge* [library *MuMIn* (Bartón 2012)], excluding combinations that included the quadratic term of a variable and did not also include the linear term of that variable. A best model subset was identified using ΔQAICc <2. For each taxon and response variable, we calculated the RVI of each of the variables in the best model subset. Collinear variables were excluded by first checking Spearman's correlations and multicollinearity (with the Variance Inflation Factor - VIF) between all independent variables included in the best model subset. VIF was tested with the R package *usdm* (Naimi 2013). If models had variables with absolute Spearman's rho > 0.5 we updated the models by removing

the correlated variable that had the lower RVI or, if RVIs were equal, removing the correlated variable with higher VIF. 4) we calculated an averaged 'combined' model for each taxon and response variable using the best subset of models that excluded collinear variables (Burnham and Anderson 2002). Statistical analyses were performed in R 3.0.3 (R Core Team, 2014).

Phylogenetic analyses

Phylogenetic relationships among species can result in over-estimation of the degrees of freedom in biogeographic analyses. Therefore, we checked the significance of model coefficients of the traits included into combined models by performing phylogenetic generalized least squares ['PGLS' (Freckleton et al. 2002)]. If combined models contained variables that were not significant in the PGLS we updated the non-phylogenetic models maintaining only the variables that were significant according to the PGLS ('final' combined models). Details on the sources of the phylogenies are described in Appendix S3. Phylogenetic analyses were performed in R using the packages *ape* (Paradis et al. 2004) and *caper* (Orme et al. 2012).

Correspondence between latitude, range filling, and traits

We analysed the relationship between range filling and the latitude of species' range centroids using GLMs separately for European mammals, birds and plants (the latter data were drawn from Estrada et al. (2015)). We explored the relationship between latitude and traits by performing univariate GLMs considering latitude as the predictor and the traits of the final models (i.e. those significant in the PGLS models) as the response variable.

267

268 **Relationship between range size and range filling**

269 We compared the average values of range size and range filling between European mammals,
270 birds and plants. However, we also wanted to check if species with small range sizes [hereafter
271 'rare' species (Kunin and Gaston 1993)] tended to have lower range filling than widespread
272 species. So, we grouped species into three categories according to the size of their ranges: we
273 considered 'rare' species those that have range sizes below the median number of occurrences
274 across the taxa, 'widespread' species those that have range sizes above the 95th percentile of
275 number of occurrences across the taxa, and 'intermediate' species those that have range sizes
276 between rare and widespread species (Bradley et al. 2015). We also tested the implications of
277 classifying widespread species as those with occurrences greater the mean number of
278 occurrences for each taxa (Bradley et al. 2015). In both cases, we plotted the three categories
279 against range filling for European mammals, birds and plants (the latter from Estrada et al.
280 (2015)).

281

282 ## Results

283 **Mammals**

284 Final combined models for mammals are detailed in Table 2, and the shape of the relationship
285 between range filling and each explanatory variable in the context of the final combined
286 models, is shown in Fig. 1. Results show that habitat generalists and early reproducing
287 mammals show the greatest range filling. Habitat breadth, sexual maturity age and trophic
288 level explained the greatest deviance in the univariate models and were therefore treated as
289 core variables (Table S2.1 Appendix S2). For the multivariate models containing both core and

candidate variables, the core variables habitat breadth and sexual maturity age were always retained (for both range filling100 and range filling95, Table S2.2 Appendix S2). Other variables retained (with RVI > 0.5) were sleep behaviour, longevity and migratory status (the latter trait for range filling100 but not range filling95). Longevity was correlated with sexual maturity age and migratory status (Table S2.5 Appendix S2), and sexual maturity age was retained (see Methods). Combined models then contained three variables (habitat breadth, sexual maturity age and sleep behaviour) (Tables S2.3 and S2.4 Appendix S2). However, sleep behaviour was not significant in the PGLS analysis (Table S3.1 Appendix S3), and therefore we excluded this trait from the final combined models. Thus, final combined models for mammals were performed with habitat breadth and sexual maturity age, for which 94 species had data (Rho between variables = 0.08, VIF = 1.01, Tables 2 and S2.5). The percentage of deviance explained was ≥24%.

Birds

Final combined models for birds are detailed in Table 3 and the shape of the relationship between range filling and each explanatory variable, in the context of the final models, is shown in Fig. 2. Habitat generalists with high annual fecundity, which can live longer than expected by their body size have the greatest range filling. Fecundity and longevity explained the greatest deviance in the univariate models and were therefore treated as core variables (Table S2.6 Appendix S2). For the multivariate models containing both core and candidate variables, fecundity, longevity, habitat breadth and body mass were always retained with RVI=1, and productivity was also retained with RVI > 0.6 (Table S2.7 Appendix S2). None of the variables selected to be entered into the combined models were collinear (Table S2.10 Appendix S2). In the combined models, habitat breadth, annual fecundity, longevity, body mass, and productivity were retained (Tables S2.8 and S2.9 Appendix S2). However, annual

315 productivity and body mass were not significant in the PGLS analysis (Table S3.2 Appendix S3),
316 and therefore we excluded these traits from the final combined models. Thus, final combined
317 models for birds were performed with habitat breadth, annual fecundity and longevity, for
318 which 282 species had data (Table 3, Rho ≤ 0.13, VIF ≤ 1.02, Table S2.10 Appendix S2).
319 Percentage of deviance explained was ≥30%.

320

321 **Range filling and latitude**

322 For mammals, birds, and plants the species with the greatest range filling were those whose
323 range centroid falls in the latitudinal centre of Europe (Fig. 3). We obtained significant
324 relationships with latitude for the following traits: habitat breadth and allometric sexual
325 maturity age for mammals (unimodal and negative relationships, respectively); annual
326 fecundity (log-transformed) and allometric longevity for birds (unimodal relationships); and
327 habitat breadth, dispersal distance, seed bank persistence and specific leaf area for plants
328 (positive relationship for habitat breadth, unimodal relationships for the other traits). A
329 positive relationship means that a higher value of a trait corresponded to a more northerly
330 range centroids, whereas a unimodal relationship means that species with a higher value of a
331 trait tend to have range centroids in the centre of Europe. Results of the models are shown in
332 Table S2.11 Appendix S2, and relationships in figures S2.2-S2.4 Appendix S2.

333

334 **Range size and range filling**

335 Breeding birds filled more of their potential range than plants and mammals. These results
336 were consistent either if we considered all species of the taxa together (Fig. S2.5 Appendix S2)

or if we divided them into rare, intermediate and widespread species with any of the classification methods (Fig. 4, Fig. S2.6 Appendix S2).

Discussion

Although we tested traits related to the four stages of the range-shift process, i.e., emigration, movement, establishment and proliferation (Estrada et al. 2016b), only traits related to the two latter stages seem to be important in determining range filling of European mammals and birds. Specifically, important traits selected for birds and mammals belong to three of the trait categories defined by Estrada et al. (2016b): ecological generalization, reproductive strategy, and persistence under unfavourable conditions (Table 1).

The importance of ecological generalization traits in determining climatic range filling is consistent with previous findings obtained for different groups of species (Thompson et al. 1999, Mattila et al. 2011, Laube et al. 2013b, Estrada et al. 2015). Ecological generalization is related to the stages of establishment and proliferation in the range-shift process by increasing resource availability (Angert et al. 2011, Estrada et al. 2016b). Broader habitat preferences could increase range filling by increasing the habitat available to be occupied, and/or because increased habitat availability provides more routes for expansion from glacial refugia (Estrada et al. 2015). During post-glacial range expansion, ecological generalization could have favoured establishment success [as observed in introduced species (Cassey et al. 2004, Sol et al. 2005)], and could have increased population trends [assisting proliferation (Jiguet et al. 2007)]. Thus, overcoming of small population problems could be a mechanism underlying the patterns documented here, and assist range shifts under climate change.

359 Regarding reproductive strategy, the observed high range filling in mammals and birds with
360 fast life histories (e.g. high fecundity, low age at maturity) might occur because fecundity
361 compensate for high mortality (Purvis et al. 2000). Like ecological generalization, reproductive
362 strategy is related to the stages of establishment and proliferation (Estrada et al. 2016b).
363 Species with fast life histories could therefore be particularly likely to colonise newly
364 climatically suitable areas as climate changes (Perry et al. 2005, Bradshaw et al. 2014), and
365 thus be less threatened by climate change than other species. However, it should be noted
366 that having a slow life history could buffer a species from environmental change within their
367 current range. Therefore if climate becomes unsuitable, species with slow life histories might
368 undergo range contractions less rapidly than species with fast life histories.

369 Bird species living longer than expected by their body size have high range filling. Longevity is
370 related to the establishment stage of the range-shift process (Estrada et al. 2016b), and the
371 relationship between longevity and range filling is that long-lived species can better persist in
372 unfavourable conditions. Long-lived species can skip a reproductive event when conditions are
373 not suitable, and still maintain a viable population. This could be particularly important when
374 colonising areas that are becoming newly suitable under climate change, in which conditions
375 can fluctuate between suitable and unsuitable. Following our results (Table 3, Fig. 2), it could
376 be that, among bird species with faster life histories, those living longer will have more
377 opportunities to produce a high number of offspring and to persist in unfavourable conditions,
378 There is often a trade-off between life-history speed and longevity, suggesting that species
379 with intermediate values for both traits might be well positioned to colonise newly suitable
380 areas under climate change (Trakimas et al. 2016).

381 Although we did not find relationships between range filling and traits related to movement
382 ability or site fidelity in birds or mammals, Estrada et al. (2015) found that movement ability
383 corresponded to range filling of European plants. Unfortunately, quantitative measurements

384 of dispersal were not available for birds and mammals, which meant we had to use indirect
385 proxies (i.e. migration and home range). This may have obscured the importance of movement
386 ability. With respect to site fidelity traits, our results are in accordance to those of Estrada et
387 al. (2016b) who found that these traits were the least-supported for range shifts (although
388 they were also very little studied).

389 Regarding the relationship of latitude with range filling (Fig. 3), contrary to our expectations
390 we found that species with higher range filling are those whose range centroids fall in the
391 centre of Europe. This pattern can be due to multiple, non-exclusive explanations. The mid-
392 domain effect (Colwell and Lees 2000) means that species with centroids in the central part of
393 the continent can potentially expand in any direction without sea-border limitations. Indeed,
394 species with centroids in central Europe have the largest geographic ranges (Fig. S2.1 Appendix
395 S2). Additionally, within a bounded geographic area the larger a species' range size the smaller
396 the area remains where the species is absent. Thus very widespread species will necessarily
397 have high range filling (which we observed, fig. 4). Alternatively, occupancy of climatically
398 suitable areas depends on the existence of suitable habitat, and climate in the centre of
399 Europe is associated with habitat types that are more homogenous than those in the south or
400 the north (Rivas-Martínez et al. 2004). Thus species that can tolerate central European climate
401 conditions will have larger amounts of habitat available to them than species elsewhere.
402 Another explanation is that unfilling of the potential ranges of species within northern or
403 southern European regions is due to the effects of biotic interactions and specifically, to the
404 presence of better adapted competitors within the unfilled portions of their ranges. Last but
405 not least, southerly species may have undergone less post-glacial expansion than they could
406 have climatically, i.e. these species have potential climate space in the north that they have
407 not colonised (Nogués-Bravo et al. 2014). Northern European species are unlikely to have had
408 their geographic ranges restricted by limited dispersal away from glacial refugia, which are
409 typically thought to have occurred in Southern Mediterranean Europe. But it could be that

410 northerly species had other refugia located in the central or northern part of Europe (e.g.
411 Fedorov and Stenseth 2001, Flagstad and Roed 2003, Brunhoff et al. 2006). Therefore
412 northerly species that underfill their potential ranges could have experienced limited post-
413 glacial range expansion. The limitation of expansion of southern and northern species could be
414 caused by geographical barriers such as mountain ranges, rivers or large extents of unsuitable
415 habitat (e.g. Lorenzini and Lovari 2006, Ricanova et al. 2013), but also by a lack of traits that
416 facilitate emigration, movement, establishment and proliferation in new environments.
417 Indeed, the traits of species with centroids in the latitudinal centre of Europe have traits are
418 related to higher range filling: central European mammals are habitat generalists, central
419 European birds have relatively high fecundity and longevity, and central European plants can
420 disperse the furthest, have long-term persistent seed banks and high specific leaf area (Estrada
421 et al. 2015) (Table S2.11, Figs. S2.2-S2.4 Appendix S2).

422 Range filling for plants is lower than that of mammals, which in turn is lower than that of birds
423 (Fig. 4, Figs. S2.5 and S2.6 Appendix S2). The high level of climatic disequilibrium for plants
424 suggests that plant ranges are much more limited by non-climatic factors than birds and
425 mammals. It may be that plants are less likely or slower to colonise new areas (García-Valdés
426 et al. 2013) and so have undergone less post-glacial range expansion than birds and mammals.
427 Indeed, the range centroids of rare plants are significantly more southerly than range centroids
428 of rare mammals, which are significantly more southerly than the range centroids of birds, a
429 pattern which breaks down for widespread species (Table S2.12). Another explanation could
430 be that climate directly limits plant distributions less than birds and mammals. So, studying
431 non-climatic range limitations could be particularly important for plants.

432 Range size and range filling were highly correlated (Spearman's rho > 0.9 for all studied
433 mammals and birds, and rho > 0.8 for plants), and rare species always had the lowest range
434 filling (Fig. 4). Range filling and range size are expected to be correlated since the potential

range size is calculated based on climate in the observed range, which increases with range size. However, it is worth noting that our analysis includes only native range. The potential range calculated using species naturalised ranges is often much larger (Early and Sax 2014), which may alter the relationship between range filling and range size. In any case, the correlation between range size and range filling is far weaker for rare species (i.e., those that have range sizes below the median number of occurrences across the taxa) than more widespread species, particularly for plants (table 4). Thus rare species show a high degree of variation in climatic disequilibrium. This may be because many species with narrow geographic ranges face substantial non-climatic range limitations (Early and Sax 2014), while others are climate specialists. While species with narrow geographic ranges have often been thought to be particularly vulnerable to climate change (Foden et al. 2013), if many of these species are relatively unlimited by climate, they could be relatively unaffected by the direct effects of climate change itself. However, for those narrowly distributed species that do experience a strong change in the climatic suitability of their ranges, they could be prevented from shifting their geographic range by strong non-climatic limitations. Low range filling could therefore indicate positive or negative outcomes for species with narrow ranges under climate change (Gaston and Fuller 2009). While space constraints could reduce variation and increase correlation between range size and range filling for widespread species, the high degree of variation in widespread species suggests this artefact does not influence the difference in the correlations between rare and widespread species (Fig. 4)

Given the importance of non-climatic range limitations in determining species responses to climate change, measuring the correlation between range filling and predictive traits could be informative by suggesting potential mechanisms of range limitation. For example, if movement ability is a major cause of range limitation, then populations may be capable of surviving in a broader range of climate conditions than currently occupied, but have simply not dispersed to locations with these conditions. In this case, current populations may be unaffected by climate

change (Sax et al. 2013). On the other hand, range limitations by negative inter-specific interactions could deplete populations if the interacting species shifts its distribution to overlap with the focal species (Sax et al. 2013). This scenario might be indicated by traits that confer a poor ability to establish or proliferate (rather than embark or disperse), e.g. traits that correspond to susceptibility to interspecific interactions (Laube et al. 2013a). All in all, our results support the convenience of using predictive traits to identify which species will be more vulnerable to future climate change. While generalist, prolific, widely-distributed and long-living species are predicted to be resilient to changes, specialists with narrow distributions and slower reproductive strategies may be at a higher risk.

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Table 1. Predictive traits used in the present study and their relationships with the four stages of the range-shift process and the seven trait categories proposed by Estrada et al. (2016b).

Range-shift stage	Trait category	Trait name
Emigration	Site fidelity	Migratory status
		Breeding behaviour[b]
Movement	Movement ability	Migratory status
		Migration distance[b]
		Home range[m]
Establishment	Avoidance of small population effects	Breeding behaviour[b]
		Group[m]
	Persistence under unfavourable conditions	Longevity
		Sleep behaviour[m]
		Hide behaviour[m]
Establishment and Proliferation	Reproductive strategy	Annual fecundity
		Annual productivity
		Body mass
		Sexual maturity age
		Inter-birth interval[m]
	Ecological generalisation	Habitat breadth
		Diet breadth
		Trophic level
		Brain size
	Competitive ability	Brain size
		Population density[b]

b: traits available just for birds. m: traits available just for mammals.

Table 2. Final combined models for **mammals**. Note that only one model was selected in the best model subset (the second best model had a ΔQAICc > 7). β: model coefficients; SE: standard errors; RVI: relative variable importance; Sig: significance: ***<0.001, **<0.01, *<0.05, ns: not significant. DE: percentage of deviance explained. Units of variables are detailed in Appendix S1.

	Range filling100 (n=94)				**Range filling95 (n=94)**			
	β	**SE**	**RVI**	**Sig**	**β**	**SE**	**RVI**	**Sig**
Intercept	-1.27	0.27		***	-1.18	0.28		***
Habitat breadth	0.26	0.06	1	***	0.25	0.06	1	***
Allometric sexual maturity age	-0.28	0.09	1	**	-0.30	0.10	1	**
DE	24.62				23.88			

Table 3. Final combined models for **birds**. Note that only one model was selected in the best model subset (the second best model had a ΔQAICc > 15). β: model coefficients; SE: standard errors; RVI: relative variable importance; Sig: significance: ***<0.001, **<0.01, *<0.05, ns: not significant. Units of variables are detailed in Appendix S1.

	Range filling100 (n=282)				**Range filling95 (n=282)**			
	β	**SE**	**RVI**	**Sig**	**β**	**SE**	**RVI**	**Sig**
Intercept	-2.01	0.25		***	-1.95	0.26		***
Habitat breadth	0.18	0.04	1	***	0.17	0.04	1	***
Log(Annual fecundity)	0.86	0.10	1	***	0.87	0.11	1	***
Allometric longevity	0.87	0.14	1	***	0.86	0.15	1	***
Percentage of deviance explained	31.29				29.62			

Table 4. Spearman's rho correlation coefficients between range size and range filling95 for rare, intermediate, and widespread European birds, mammals, and plants. Stars indicate significance: ***<0.001, **<0.01, *<0.05

	Birds	Mammals	Plants
Rare	0.65***	0.57***	0.29***
Intermediate	0.96***	0.94***	0.90***
Widespread	0.94***	0.79*	0.78***

Figure 1. Regression lines for the effects of habitat breadth (a) and allometric sexual maturity age (b) on range filling95 for mammals. Regression coefficients were obtained by modelling the two explanatory variables simultaneously.

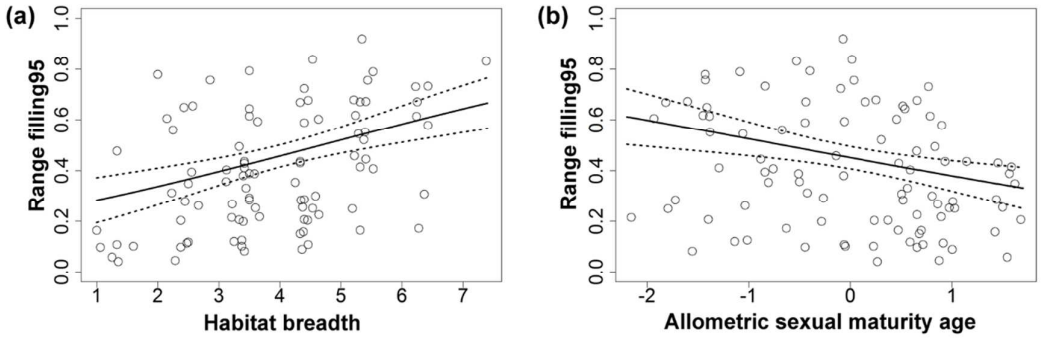


Figure 2. Regression lines for the effects of habitat breadth (a), fecundity (b) and longevity (c) on range filling95 for birds. Regression coefficients were obtained by modelling the three explanatory variables simultaneously.

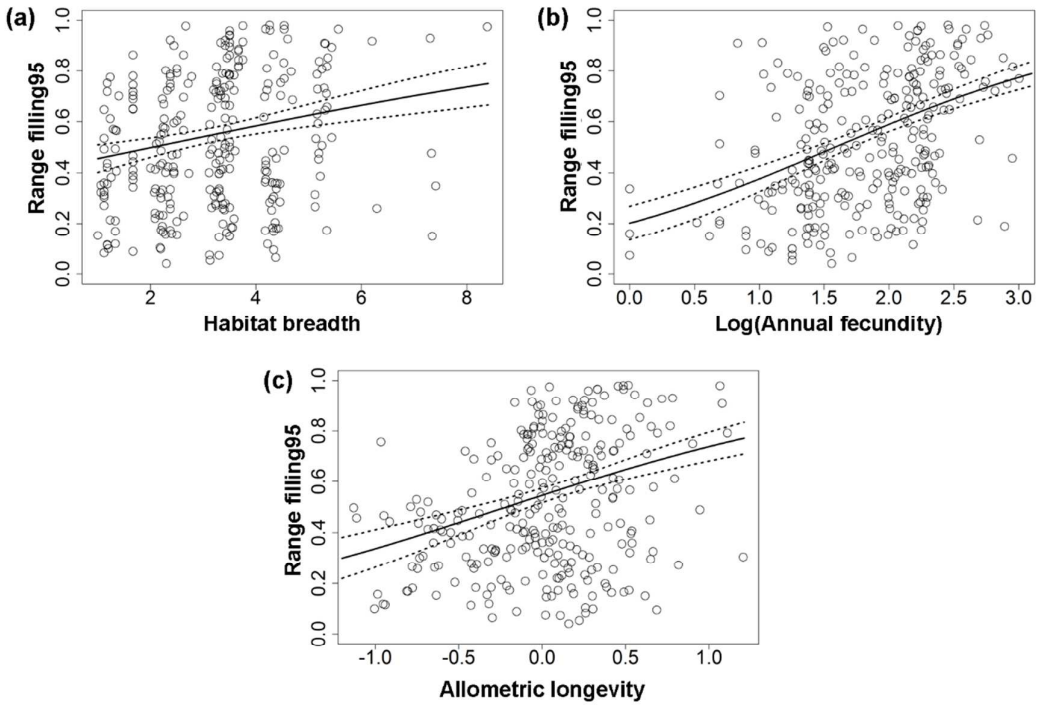


Figure 3. Relationship of latitude with range filling95 of plants (a), mammals (b) and birds (c).

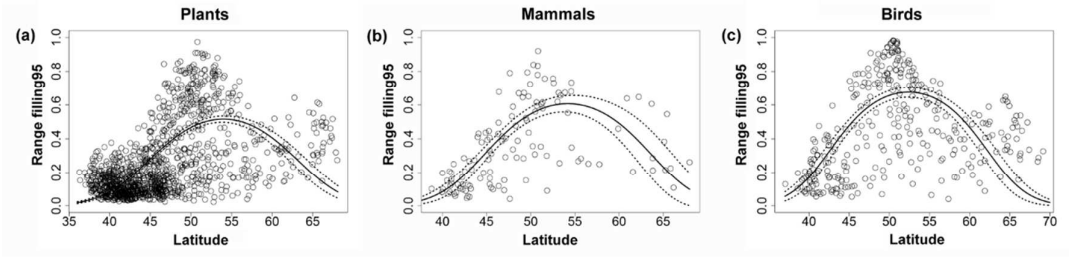
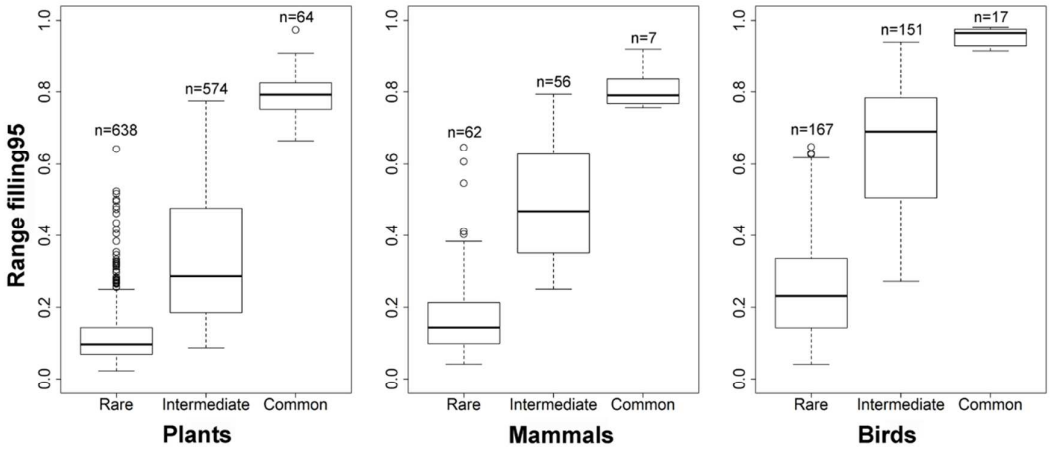


Figure 4. Range filling95 for rare, intermediate and widespread species of European plants, mammals and breeding birds. 'Rare' species are those that have range sizes below the median number of occurrences across the taxa, 'widespread' species those that have range sizes above the 95th percentile of number of occurrences across the taxa, and 'intermediate' species those that have range sizes between rare and widespread species. Boxes show the lower and upper quartiles and the median value. Whiskers show either the maximum and minimum values or 1.5 times the interquartile range (whichever is closer to the box). Dots represent values outside the range of 1.5 times the interquartile range. n is the sample size of each of the groups.



What can life-history traits tell us about species' range-shift responses to climate change? A multi-taxon approach

Alba Estrada, Ignacio Morales-Castilla, Catarina Meireles, Paul Caplat and Regan Early

Appendix S1. Description of species' predictive traits, and sources used to compile them.

Description of species' predictive traits for mammals and birds related to emigration, movement, establishment, and proliferation

See below the description for all the traits. The rationale of using each trait is included in the main text. We log-transformed (natural logarithm) some traits for analysis to reduce heteroscedasticity (see below). For some traits we considered the allometric effect with respect to body mass. In these cases it is not the trait *per se* which we hypothesize to affect range filling but the extent to which the effect of the trait is either larger or smaller than that expected for a given body size (Sol et al. 2012). We calculated the residuals of a log-log least-squares linear regression of the trait in question against body mass. These residuals were considered the values of the trait. To differentiate the names of these traits we used the word "Allometric" prior to the name of the trait (Sol et al. 2012) (see below).

- *Migratory status*: We classified species as migrants (even if only occasionally) or non-migrants.

- *Migration distance*: We collected migration distance (in km) from Végvári et al. (2010) who estimated it as the orthodrome (great circle) distance between the midpoint values of longitudes and latitudes occupied in the summer and winter distributions. We used a zero value for non-migrant species.

- *Breeding behaviour*: We used two possible values for this trait: colonial if nesting in clusters and territorial otherwise.

- *Allometric home range*: Home range is defined as the size of the area within which everyday activities of individuals are typically restricted (Jones et al. 2009). We used the mean value (in individuals/km^2) for each species to calculate the allometric trait.

- *Group*: We used two possible values for this trait: living in groups *vs* solitary.

- *Allometric longevity*: We used the maximum longevity value (in years and months for birds and mammals, respectively) recorded for each species to calculate the allometric trait.

- *Sleep behaviour* and *Hide behaviour*: We classified as sleepers those species having hibernation or daily torpor; and as hiders those species using burrows, chambers, dens, tunnels, tree holes, or caves (Liow et al. 2009). We established two categories for these two traits: yes and no.

- *Clutch/litter size*: Slow life-history (small clutches/litters) or low fecundity are associated with higher vulnerability to extinction (Purvis et al. 2000, Triviño et al. 2013). We therefore

hypothesise that species with larger clutch/litter sizes are better able to proliferate following colonisation. We considered the mean value for each species. However, we did not enter this trait into models because we used it to calculate *fecundity* and *productivity* (see below).

- *Number of clutches/litters per year*: We hypothesize that species with more broods or litters per year would have advantages to establish and proliferate. Species with the capacity to have multiple clutches/litters per year are better able to synchronize with peaks of food abundance, which improves reproductive success (Jiguet et al. 2007, Triviño et al. 2013). Small brood numbers have been associated with population declines (Jiguet et al. 2007). We used the mean value for each species. We did not enter this trait into models because we used it to calculate *fecundity* and *productivity* (see below).

- *Annual fecundity*: Calculated as the product of clutch or litter size and the number of clutches/litters per year. We log-transformed (natural logarithm) this trait for analysis.

- *Annual productivity*: Calculated as the ratio between clutches/litters per year and clutch/litter size. It represents the reproductive strategy of the species. For example, a species that has four clutches in a year with two individuals each will have the same *fecundity* as a species having two clutches with four individuals each, whereas *productivity* will differ. High *productivity* will correspond to species that have many clutches throughout the year with low number of individuals and *vice versa*. We log-transformed this trait for analysis.

- *Body Mass*: We used the mean value (in grams) for each species and log-transformed this trait for analysis.

- *Allometric sexual maturity age*: We used the minimum value (in days) recorded for each species to estimate the allometric trait.

- *Inter-birth interval*: We used the mean value (in days) for each species and log-transformed this trait for analysis.

- *Habitat breadth*: We compiled the general habitat (e.g., 'forest') and primary sub-habitat categories (e.g. 'boreal' or 'temperate' forest) within which each species is associated according to the Habitat Classification Scheme of the IUCN (http://www.iucnredlist.org/). We calculated a habitat breadth index using an integer value of the number of general habitats a species occupies, and a decimal figure that represents the ratio of sub-habitats it occupies (i.e., if a species lives in three general habitats and in four out of ten possible sub-habitats for those general habitats, it was assigned an index value of 3.4). To estimate the habitat breadth index, we only considered terrestrial surface habitats that appear in Europe. In the case of birds, the IUCN classification differentiates between breeding and non-breeding habitats. As the distribution data are of breeding pairs, we only consider breeding habitats.

- *Diet breadth*: We calculated diet breath as an ordinal trait consisting of the sum of the following 8 diet types: vertebrate, invertebrate, fruit, flowers/nectar/pollen, leaves/branches/bark, seeds, grass, and roots/tubers (Jones et al. 2009, Clarke and O'Connor 2014).

- *Trophic level*: We used this trait as a categorical variable with four classes: herbivore, carnivore - mainly vertebrates, carnivore - mainly invertebrates, and omnivore (Gregory et al. 2007).

- *Allometric brain size*: We used the mean value (in grams) for each species to estimate the allometric trait. For species for which brain mass was not available, we used the average brain

residual of the species from the same genus provided real data exist for at least three species (Sol et al. 2012).

- *Allometric population density*: We used the maximum value (in breeding pairs/km^2) recorded for each species to estimate the allometric trait.

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Sources used to compile the analysed traits

Trait	Source
Migratory status*	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Migration distance	20
Breeding behaviour	1, 7, 9, 14, 15, 21, 49, 101
Home range	1, 23, 35, 100
Group	1, 3, 32, 45, 67
Longevity	1, 3, 6, 8, 17, 20, 21, 23, 39, 40, 49, 50, 53, 54, 55
Sleep behaviour	1, 3, 4, 5, 9, 22, 32, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90
Hide behaviour	1, 3, 4, 5, 9, 32, 33, 34, 91, 92, 93, 94, 95, 96, 97, 98, 99
Clutch/litter size	1, 3, 6, 7, 17, 23, 32, 39, 40, 41, 42
Clutches/litters per year*	1, 3, 6, 7, 17, 23, 32, 39, 40, 43
Body Mass	1, 3, 6, 7, 8, 12, 14, 17, 20, 21, 23, 32, 35, 36, 37, 39, 41, 43, 44, 45, 46, 47, 48, 49, 50, 51
Sexual maturity age	1, 3, 7, 20, 23, 32, 39, 41, 49, 50, 52
Inter-birth interval	23, 39
Habitat breadth	4
Diet breath*	1, 3, 5, 6, 9, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31
Trophic level*	1, 3, 5, 6, 9, 10, 15, 21, 22, 23, 24, 27, 28, 30, 31, 32, 33, 34, 35, 36, 37, 38
Brain size	43, 47, 53, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66
Population density	102

* Expert opinion were also used to classify species or to correct some misclassifications. Consulted experts: F. Carvalho (University of Évora, Portugal) and J. Martínez-Padilla (UMIB, UO-CSIC-PA, Spain).

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What can life-history traits tell us about species' range-shift responses to climate change? A multi-taxon approach

Alba Estrada, Ignacio Morales-Castilla, Catarina Meireles, Paul Caplat and Regan Early

Appendix S2. Additional tables and figures.

Table S2.1. Results of univariate models for range filling of **mammals**. +: positive relationship, -: negative relationship, x: categorical variable, ∩: concave downward relationship of the quadratic term. The percentage of deviance explained by the model is in parentheses. A variable followed by a superscript 2 indicates the quadratic term. Traits are sorted according to decreasing deviance explained. Cells shaded grey indicate traits with $P < 0.25$, i.e., candidate traits for the first multivariate models. Units can be found in Appendix S1. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, ns: $P > 0.05$.

	Number of species	Range filling100	Range filling95
Habitat breadth	125	+ *** (19.6)	+ *** (18.8)
Habitat breadth^2	125	ns	ns
Allometric sexual maturity age	94	- ** (10.3)	- *** (10.8)
Allometric sexual maturity age^2	94	ns	ns
Trophic level	116	x ** (10.04)	x ** (8.19)
Migratory status	85	- ** (8.84)	- * (7.19)
Sleep behaviour	120	- *** (9.68)	- ** (7.85)
Diet breadth	116	+ * (4.04)	+ * (3.23)
Diet breadth^2	116	ns	ns
Allometric longevity	99	ns	ns
Allometric longevity^2	99	∩ * (5.06)	∩ * (4.38)
Log(Annual fecundity)	102	+ * (5.28)	+ * (5.04)
Log(Annual fecundity)^2	102	ns	ns
Group	77	- * (4.97)	ns p=0.07
Log(Body mass)	121	ns p=0.09	ns p=0.19
Log(Body mass)^2	121	ns	ns
Log(Annual productivity)	102	ns p=0.2	ns

Log(Annual productivity)^2	102	ns	ns
Hide behaviour	123	ns	ns
Log(Inter-birth interval)	59	ns	ns
Log(Inter-birth interval)^2	59	ns	ns
Allometric brain	65	ns	ns
Allometric brain^2	65	ns	ns
Allometric Home range	56	ns	ns
Allometric Home range^2	56	ns	ns

Table S2.2. First round of multivariate models for **mammals**. Models are performed with the variables that in the univariate models accounted for more than 10% of the explained deviance together with one of the explanatory variables for which P < 0.25 in the univariate models, i.e., core and candidate variables. Depending on the response variable these are three or four-variable models. For each set of variables, results are averaged across the best model subset (i.e. ΔQAICc < 2). β: model-averaged coefficients; SE: standard errors across best model subset; RVI: relative variable importance; N: sample size. In trophic level the different categories are: Herb: herbivore, CarV: carnivore - mainly vertebrates, CarIn: carnivore - mainly invertebrates, Omni: omnivore. Rows shaded grey correspond to variables with *RVI* > 0.5, and therefore they are considered in the final combined models. Units of variables are detailed in Appendix S1.

Range filling100

	Range size			
	β	**SE**	**RVI**	**N**
Intercept	-1.16	0.1		76
Habitat breadth	0.26	0.01	1	
Allometric sexual maturity age	-0.30	0.04	1	
Trophic level	-	-	-	
Migratory status	-0.41	0.02	0.6	
Intercept	-0.73	0.07		91
Habitat breadth	0.21	0.01	1	
Allometric sexual maturity age	-0.19	0.02	0.74	
Trophic level (CarV)	-0.20	0.03	0.26	
Trophic level (Herb)	-0.59	0.02	0.26	
Trophic level (Omni)	-0.03	0.02	0.26	
Sleep behaviour	-0.64	0.08	1	
Intercept	-1.35	0.09		92
Habitat breadth	0.26	0.00	1	
Allometric sexual maturity age	-0.27	0.02	1	
Trophic level	-	-	-	
Diet breadth	0.05	0.00	0.4	
Intercept	-1.16	0.05		86
Habitat breadth	0.24	0.01	1	
Allometric sexual maturity age	-0.33	0.06	1	
Trophic level	-	-	-	
Allometric longevity	0.22	0.01	0.6	
Allometric longevity2	-0.11	0.01	0.21	
Intercept	-1.17	0.27		85
Habitat breadth	0.24	0.06	1	
Allometric sexual maturity age	-0.27	0.09	1	
Trophic level	-	-	-	
Annual fecundity (log)	-	-	-	
Intercept	-1.16	0.04		65

Habitat breadth	0.25	0.01	1	
Allometric sexual maturity age	-0.36	0.02	1	
Trophic level	-	-	-	
Group	-0.20	0.01	0.32	
Intercept	-1.29	0.04		93
Habitat breadth	0.25	0.00	1	
Allometric sexual maturity age	-0.28	0.01	1	
Trophic level	-	-	-	
Body mass (log)	0.02	0.00	0.3	
Intercept	-1.18	0.03		85
Habitat breadth	0.24	0.00	1	
Allometric sexual maturity age	-0.27	0.01	1	
Trophic level	-	-	-	
Annual productivity (log)	-0.10	0.01	0.29	

Range filling95

	Range size			
	β	**SE**	**RVI**	**N**
Intercept	-1.17	0.28		93
Habitat breadth	0.25	0.06	1	
Allometric sexual maturity age	-0.30	0.10	1	
Trophic level	-	-	-	
Intercept	-1.12	0.09		76
Habitat breadth	0.26	0.01	1	
Allometric sexual maturity age	-0.33	0.03	1	
Migratory status	-0.36	0.02	0.49	
Intercept	-0.73	0.03		92
Habitat breadth	0.21	0.00	1	
Allometric sexual maturity age	-0.20	0.01	0.71	
Sleep behaviour	-0.56	0.07	1	
Intercept	-1.24	0.07		92
Habitat breadth	0.26	0.00	1	
Allometric sexual maturity age	-0.30	0.01	1	
Diet breadth	0.04	0.00	0.33	
Intercept	-1.07	0.05		87
Habitat breadth	0.24	0.01	1	
Allometric sexual maturity age	-0.37	0.07	1	
Allometric longevity	0.27	0.01	0.69	
Allometric longevity2	-0.11	0.01	0.22	
Intercept	-1.08	0.28		86

Habitat breadth	0.24	0.06	1	
Allometric sexual maturity age	-0.29	0.10	1	
Annual fecundity (log)	-	-	-	
Intercept	-1.08	0.04		65
Habitat breadth	0.25	0.01	1	
Allometric sexual maturity age	-0.40	0.02	1	
Group	-0.17	0.02	0.29	
Intercept	-1.18	0.28		94
Habitat breadth	0.25	0.06	1	
Allometric sexual maturity age	-0.30	0.10	1	
Body mass (log)	-	-	-	

Table S2.3. Best model subset for the combined models for **mammals** (i.e. ΔQAICc < 2) before taking into account phylogenetic relationships. Weights: Akaike weights. +: positive coefficient; -: negative coefficient; x: categorical variable.

	Variables					
	Habitat breadth	**Allometric sexual maturity age**	**Sleep behaviour**	**QAICc**	**ΔQAICc**	**Weights**
Range filling100	+	-	-	107.5	0	0.625
	+		-	108.5	1.02	0.375
Range filling95	+	-	-	107.5	0	0.709
	+		-	109.3	1.78	0.291

Table S2.4. Combined models for **mammals** before taking into account phylogenetic relationships. For each set of variables, results are averaged across the best model subset (i.e. ΔQAICc < 2). β: model-averaged coefficients; SE: standard errors across best model subset; RVI: relative variable importance; −CI and +CI, confidence limits for coefficient estimates at the 95% confidence interval (CI). DE: percentage of deviance explained. Units of variables are detailed in Appendix S1.

	Range filling100 (n=92)					**Range filling95 (n=92)**				
	β	**SE**	**RVI**	**-CI**	**+CI**	**β**	**SE**	**RVI**	**-CI**	**+CI**
Intercept	-0.79	0.03				-0.73	0.03			
Habitat breadth	0.21	0.00	1	0.20	0.21	0.21	0.00	1	0.20	0.21
Allometric sexual maturity age	-0.17	0.01	0.63	-0.19	-0.16	-0.20	0.01	0.71	-0.22	-0.19
Sleep behaviour	-0.61	0.07	1	-0.74	-0.47	-0.56	0.07	1	-0.71	-0.42
DE	31.27					29.36				

Table S2.5. Spearman's correlations between all pairs of life-history traits for **mammals**. Each comparison was performed with the maximum number of species for each pair of traits. L.: logarithm, A.: allometric. Trophic: trophic level, Mig: migratory status, Hider: hide behaviour, Sleeper: sleep behaviour, Diet: diet breadth, Hab: habitat breadth, Brain: brain size, Long: longevity, Sexmat: sexual maturity age, Fec: annual fecundity, Prod: annual productivity.

	Trophic	Mig	Hider	Sleeper	Diet	Hab	Group	A. Brain	L. Body mass	L. Inter-birth interval	A. Home range	A. Long	A. Sexmat	L. Fec	L. Prod
Trophic	1	-0.55	0.00	-0.33	0.84	0.05	-0.62	0.35	0.48	-0.19	0.14	-0.52	-0.45	0.41	-0.52
Mig		1	0.07	0.54	-0.45	-0.13	0.44	-0.28	-0.47	0.26	0.28	0.50	0.37	-0.48	0.25
Hider			1	0.26	-0.06	-0.12	-0.03	0.00	-0.34	-0.21	0.29	-0.02	-0.06	0.23	-0.22
Sleeper				1	-0.25	-0.03	0.36	-0.63	-0.45	0.25	-0.09	0.42	0.41	-0.40	0.25
Diet					1	0.05	-0.48	0.26	0.46	-0.25	-0.16	-0.44	-0.39	0.34	-0.43
Hab						1	0.02	0.13	0.03	0.00	0.10	0.10	-0.08	-0.01	-0.01
Group							1	-0.21	-0.23	0.25	-0.36	0.63	0.46	-0.55	0.55
A. Brain								1	0.17	-0.36	0.32	-0.26	-0.39	0.28	-0.29
L. Body mass									1	0.31	0.03	-0.07	-0.19	-0.01	-0.33
L. Inter-birth interval										1	0.61	0.72	0.77	-0.86	-0.22
A. Home range											1	0.45	0.26	-0.28	-0.46
A. Long												1	0.66	-0.74	0.34
A. Sexmat													1	-0.75	0.17
L. Fec														1	-0.28
L. Prod															1

Table S2.6. Results of univariate models for range filling of **birds**. +: positive relationship, -: negative relationship, x: categorical variable, ∩: concave downward relationship of the quadratic term. The percentage of deviance explained by the model is in parentheses. A variable followed by a superscript 2 indicates the quadratic term. Traits are sorted according to decreasing deviance explained. Cells shaded grey are the traits with $P < 0.25$, i.e., candidate traits for the first multivariate models. Units can be found in Appendix S1. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, ns: $P > 0.05$.

	Number of species	Range filling100	Range filling95
Log(Annual fecundity)	292	+ *** (14.4)	+ *** (14.2)
Log(Annual fecundity)^2	292	ns	ns
Allometric longevity	307	+ *** (12.3)	+ *** (11.52)
Allometric longevity^2	307	ns	ns
Log(Body mass)	327	- *** (7.23)	- *** (7.2)
Log(Body mass)^2	327	ns	ns
Habitat breadth	328	+ *** (5.54)	+ *** (5.19)
Habitat breadth^2	328	ns	ns
Trophic level	334	x * (3.00)	x * (3.09)
Log(Annual productivity)	292	+ * (1.78)	+ * (1.51)
Log(Annual productivity)^2	292	ns	ns
Diet breadth	333	+ * (1.47)	+ * (1.57)
Diet breadth^2	333	ns	ns
Allometric sexual maturity age	270	ns p=0.21	ns p=0.23
Allometric sexual maturity age^2	270	ns	ns
Allometric population density	226	ns p=0.19	ns p=0.2
Allometric population density^2	226	∩ * (2.45)	ns
Migration distance	155	ns	ns
Migration distance^2	155	ns	ns
Migratory status	322	ns	ns
Breeding behaviour	283	ns	ns

Allometric brain size	242	ns	ns
Allometric brain size^2	242	ns	ns

Table S2.7. First round of multivariate models for **birds**. Models are performed with the variables that in the univariate models accounted for more than 10% of the explained deviance (annual fecundity and allometric longevity) together with one of the explanatory variables for which P < 0.25 in the univariate models, i.e., core and candidate variables. Therefore, they are three-variable models. For each set of variables, results are averaged across the best model subset (i.e. ΔQAICc < 2). β: model-averaged coefficients; SE: standard errors across best model subset; RVI: relative variable importance; N: sample size. Rows shaded grey correspond to variables with *RVI* > 0.5, and therefore they are considered in the final combined models. Units of variables are detailed in Appendix S1.

		Range filling100			Range filling95		
	N	**β**	**SE**	**RVI**	**β**	**SE**	**RVI**
Intercept	287	-0.73	0.33		-0.69	0.34	
Annual fecundity (log)		0.69	0.12	1	0.70	0.12	1
Allometric longevity		0.96	0.14	1	0.94	0.14	1
Body mass (log)		-0.08	0.04	1	-0.08	0.04	1
Intercept	282	-2.01	0.25		-1.95	0.26	
Annual fecundity (log)		0.86	0.10	1	0.87	0.11	1
Allometric longevity		0.87	0.14	1	0.86	0.15	1
Habitat breadth		0.18	0.04	1	0.17	0.04	1
Intercept	286	-1.35	0.20		-1.30	0.21	
Annual fecundity (log)		0.82	0.10	1	0.83	0.11	1
Allometric longevity		0.95	0.14	1	0.94	0.15	1
Trophic level		-	-	-	-	-	-
Intercept	287	-1.22	0.09		-1.20	0.09	
Annual fecundity (log)		0.83	0.01	1	0.84	0.01	1
Allometric longevity		0.93	0.03	1	0.92	0.03	1
Annual productivity (log)		0.19	0.01	0.69	0.18	0.01	0.62
Intercept	287	-1.36	0.20		-1.32	0.21	
Annual fecundity (log)		0.82	0.10	1	0.83	0.11	1
Allometric longevity		0.96	0.14	1	0.95	0.15	1
Diet breadth		-	-	-	-	-	-
Intercept	261	-1.17	0.22		-1.10	0.22	
Annual fecundity (log)		0.74	0.11	1	0.74	0.11	1
Allometric longevity		0.95	0.15	1	0.93	0.16	1
Allometric sexual maturity age		-	-	-	-	-	-
Intercept	204	-1.37	0.24		-1.32	0.24	
Annual fecundity (log)		0.88	0.12	1	0.89	0.12	1
Allometric longevity		1.02	0.16	1	0.99	0.16	1
Allometric population density		-	-	-	-	-	-
Allometric population density2		-	-	-	NA	NA	NA

Table S2.8. Best model subset for the combined models for **birds** (i.e. ΔQAICc < 2) before taking into account phylogenetic relationships. Weights: Akaike weights. +: positive coefficient; -: negative coefficient; x: categorical variable.

	Variables							
	Habitat breadth	**Fecundity (log)**	**Allometric longevity**	**Body mass (log)**	**Productivity (log)**	**QAICc**	**ΔQAICc**	**Weights**
Range filling100	+	+	+	-		312.3	0	0.701
	+	+	+	-	+	314.0	1.7	0.299
Range filling95	+	+	+	-		311.9	0	0.713
	+	+	+	-	+	313.7	1.82	0.287

Table S2.9. Combined models for **birds** before taking into account phylogenetic relationships. For each set of variables, results are averaged across the best model subset (i.e. ΔQAICc < 2). β: model-averaged coefficients; SE: standard errors across best model subset; RVI: relative variable importance. Units of variables are detailed in Appendix S1.

	Range filling100 (n=282)					**Range filling95 (n=282)**				
	β	**SE**	**RVI**	**-CI**	**+CI**	**β**	**SE**	**RVI**	**-CI**	**+CI**
Intercept	-1.4	0.03				-1.34	0.03			
Habitat breadth	0.17	0.00	1	0.16	0.18	0.17	0.00	1	0.16	0.17
Annual fecundity (log)	0.75	0.01	1	0.73	0.76	0.75	0.01	1	0.74	0.77
Allometric longevity	0.86	0.01	1	0.84	0.88	0.85	0.01	1	0.83	0.87
Body mass (log)	-0.08	0.00	1	-0.08	-0.07	-0.08	0.00	1	-0.08	-0.07
Annual productivity (log)	0.06	0.01	0.3	0.05	0.07	0.06	0.01	0.29	0.04	0.07
Percentage of deviance explained	32.57					30.78				

Table S2.10. Spearman's correlations between all pairs of life-history traits for **birds**. Each comparison was performed with the maximum number of species for each pair of traits. L.: logarithm, A.: allometric. Trophic: trophic level, Breeding: breeding behaviour, Diet: diet breadth, Hab: habitat breadth, Mig: migratory status, Mig dist: migration distance, Brain: brain size, Popdens: population density, Long: longevity, Sexmat: sexual maturity age, Fec: annual fecundity, Prod: annual productivity.

	Trophic	Breeding	Diet	Hab	Mig	Mig dist	A. Brain	L. Body mass	A. Popdens	A. Long	A. Sexmat	L. Fec	L. Prod
Trophic	1	-0.04	0.76	0.02	-0.13	-0.33	0.00	-0.08	0.24	0.11	-0.14	0.31	0.02
Breeding		1	0.02	0.05	0.13	0.09	-0.02	0.23	-0.01	0.22	0.10	-0.11	-0.03
Diet			1	-0.08	-0.08	-0.24	-0.14	0.03	0.30	0.06	-0.21	0.25	-0.08
Hab				1	0.01	-0.02	0.21	-0.08	-0.05	0.13	-0.05	0.04	0.26
Mig					1	0.82	-0.23	-0.02	0.08	0.06	0.20	-0.04	0.10
Mig dist						1	-0.29	-0.18	0.08	0.05	0.25	-0.10	0.03
A. Brain							1	0.01	-0.28	0.13	0.07	-0.19	0.04
L. Body mass								1	0.01	0.01	-0.11	-0.44	-0.22
A. Popdens									1	0.11	0.07	0.09	-0.01
A. Long										1	0.17	0.00	0.20
A. Sexmat											1	-0.24	0.10
L. Fec												1	0.01
L. Prod													1

Table S2.11. Univariate models between relevant traits (response) and latitude (predictor) for mammals, birds and plants. Tested traits were habitat breadth and allometric sexual maturity age for mammals (see Table 2); habitat breadth, annual fecundity (log-transformed) and allometric longevity for birds (see Table 3); and habitat breadth, dispersal distance, seed bank persistence and specific leaf area for plants (see Estrada et al. 2015). Only significant relationships are shown in the table. All response variables fitted a Gaussian distribution except dispersal distance and specific leaf area that fitted a negative binomial distribution. β: model coefficients; SE: standard errors; Sig.: significance: ***<0.001, **<0.01, *<0.05.

Group	Response variable	Predictor	β	SE	Sig.
Mammals	Habitat breadth	Intercept	-16.53	5.70	**
		Latitude	0.776	0.222	***
		Latitude^2	-0.00726	0.00212	***
	Allometric sexual maturity age	Intercept	1.99	0.769	*
		Latitude	-0.0404	0.0155	*
Birds	Log(Annual fecundity)	Intercept	-4.90	1.42	***
		Latitude	0.256	0.054	***
		Latitude^2	-0.00239	0.000508	***
	Allometric longevity	Intercept	-6.22	1.04	***
		Latitude	0.241	0.040	***
		Latitude^2	-0.00229	0.000377	***
Plants	Habitat breadth	Intercept	0.610	0.239	*
		Latitude	0.0224	0.00495	***
	Dispersal distance	Intercept	-13.46	4.04	***
		Latitude	0.851	0.162	***
		Latitude^2	-0.00847	0.00162	***
	Seed bank persistence	Intercept	-12.43	2.55	***
		Latitude	0.553	0.0988	***
		Latitude^2	-0.00522	0.000954	***
	Specific leaf area	Intercept	-7.29	1.73	***
		Latitude	0.407	0.0676	***
		Latitude^2	-0.00394	0.000658	***

Table S2.12. Linear models comparing the range centroids of all, rare, intermediate, and widespread European birds, mammals, and plants. β: model coefficients; SE: standard errors; Sig: significance: ***<0.001, **<0.01, *<0.05, ns: not significant

	Mammals			Plants		
	β	**SE**	**Sig**	**β**	**SE**	**Sig**
All	-2.00	0.70	**	-4.33	0.41	***
Rare	-2.68	1.07	*	-6.37	0.62	***
Intermediate	-1.37	0.86	ns	-2.63	0.50	***
Widespread	0.00	0.70	ns	0.70	0.43	ns

Figure S2.1. Relationship of latitude with range size of plants (a), mammals (b) and birds (c).

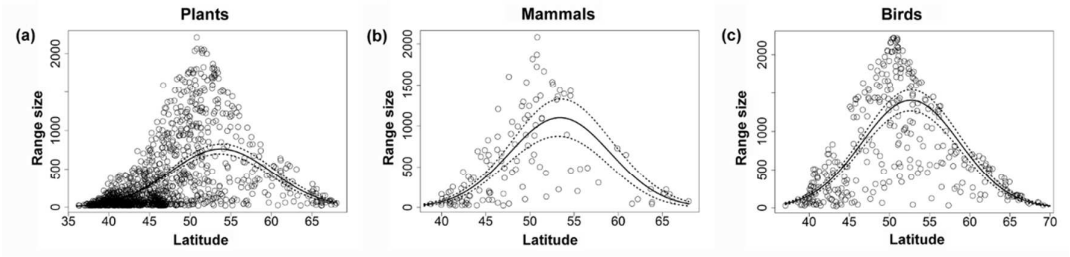


Figure S2.2. Relationships of significant univariate models between relevant traits (response) and latitude (predictor) for **mammals** (see Table S2.11).

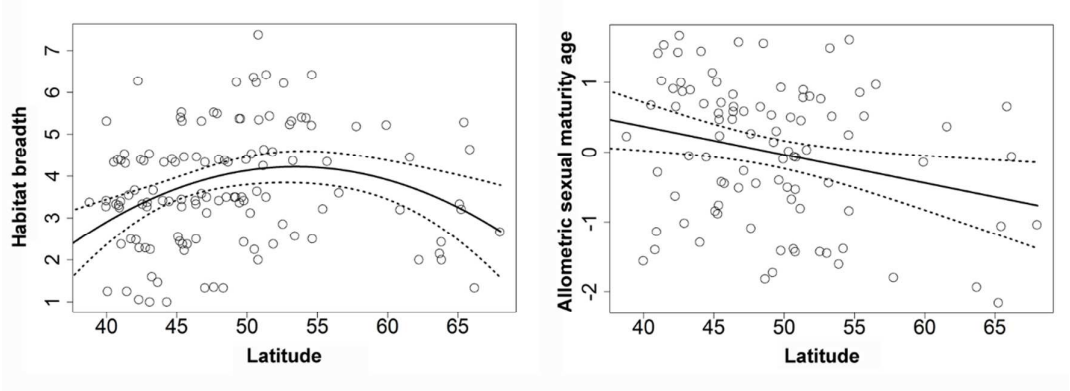


Figure S2.3. Relationships of significant univariate models between relevant traits (response) and latitude (predictor) for **birds** (see Table S2.11).

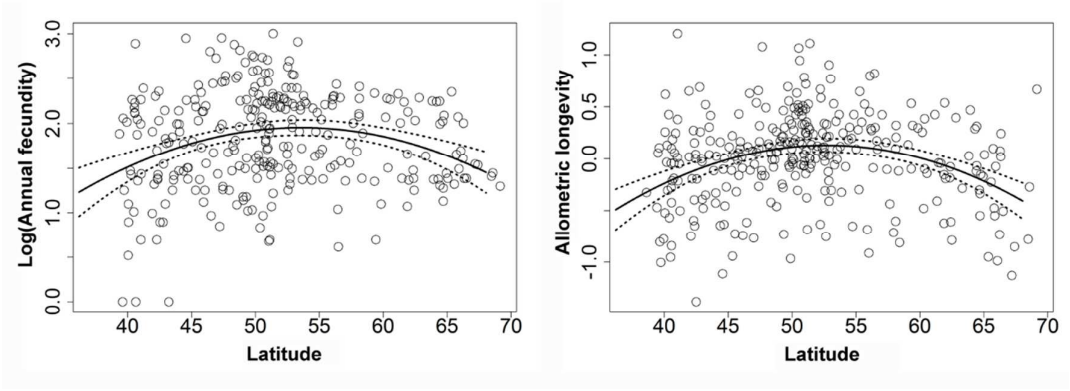


Figure S2.4. Relationships of significant univariate models between relevant traits (response) and latitude (predictor) for **plants** (see Table S2.11). Data from Estrada et al. (2015).

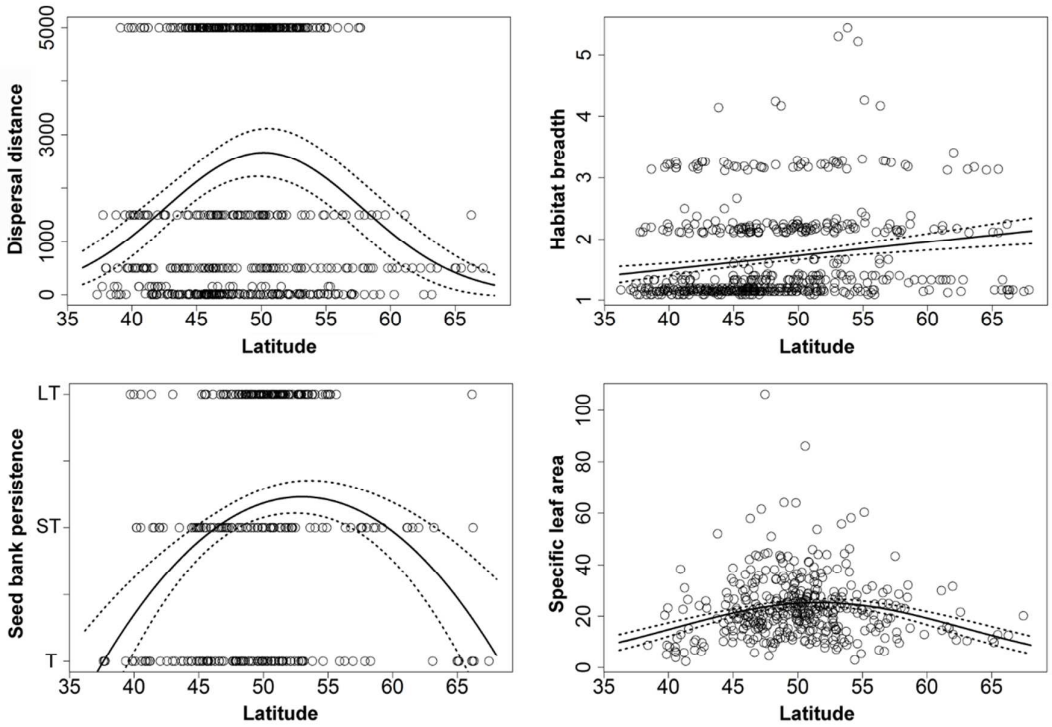


Figure S2.5. Range filling95 for European plants, mammals and breeding birds. Boxes show the lower and upper quartiles and the median value. Whiskers show either the maximum and minimum values or 1.5 times the interquartile range (whichever is closer to the box). Dots represent values outside the range of 1.5 times the interquartile range. n is the sample size of each of the groups.

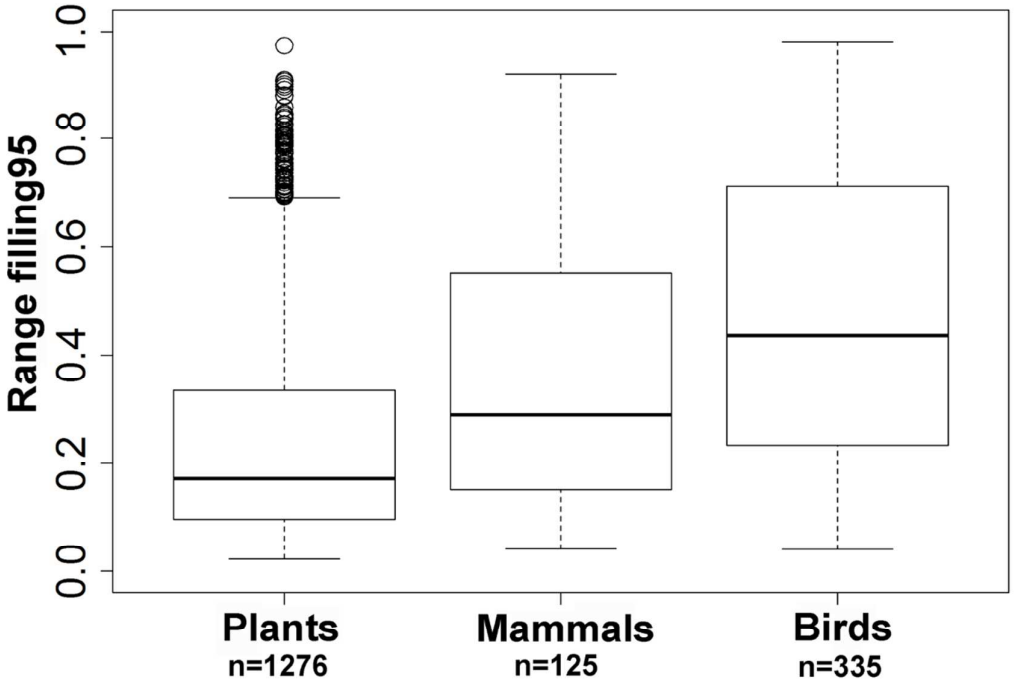
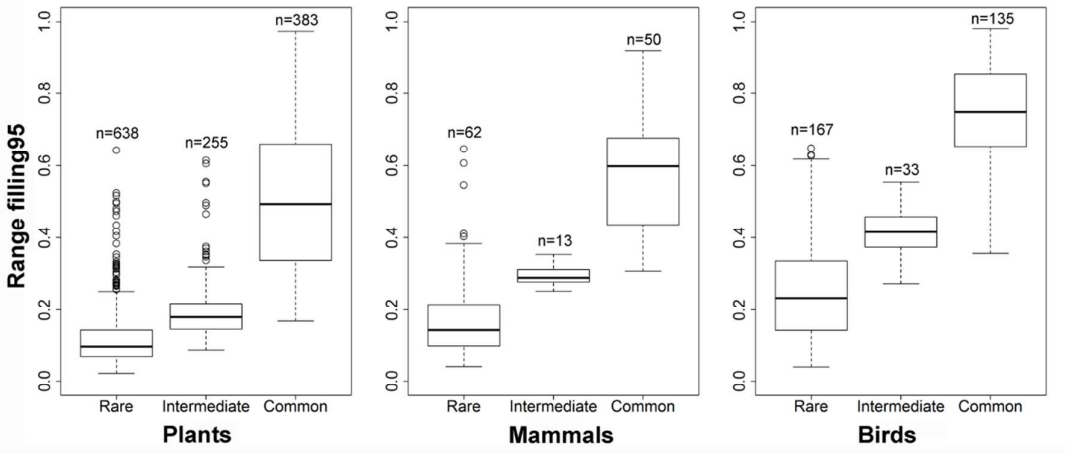


Figure S2.6. Range filling95 for rare, intermediate and widespread species of European plants, mammals and breeding birds. 'Rare' species are those that have range sizes below the median number of occurrences across the taxa, 'widespread' species those that have range sizes above the mean number of occurrences across the taxa, and 'intermediate' species those that have range sizes between rare and widespread species. Boxes show the lower and upper quartiles and the median value. Whiskers show either the maximum and minimum values or 1.5 times the interquartile range (whichever is closer to the box). Dots represent values outside the range of 1.5 times the interquartile range. n is the sample size of each of the groups.



What can life-history traits tell us about species' range-shift responses to climate change? A multi-taxon approach

Alba Estrada, Ignacio Morales-Castilla, Catarina Meireles, Paul Caplat and Regan Early

Appendix S3. Phylogenetic analyses, details, data and results.

Modelling details

Cross-species analyses (i.e. those where species represent the analysis units) should account for phylogenetic autocorrelation. Phylogenetic autocorrelation means that species cannot be considered as independent units because phylogenetically related species are phenotypically similar due to their shared ancestry (Felsenstein 1985; Grafen 1989; Martins and Hansen 1997). This means that phylogenetically proximal will tend to show more similar trait values than expected at random (Blomberg et al. 2003). If species are not independent and their phylogenetic relationships are ignored in regression models, then the degrees of freedom of parametric statistical tests will be inflated, compromising the statistical significance of model coefficients. To account for phylogenetic non-independence on our results, we re-ran the combined models for selected variables using phylogenetic generalized least squares (PGLS) (Freckleton et al. 2002) and retained only significant predictors therein. PGLS accounts for non-independence of the residuals (i.e. residual autocorrelation) by including a phylogenetic variance-covariance matrix describing the expected error structure in a Generalized Least Squares framework (Freckleton et al. 2002). PGLS can use Maximum Likelihood to estimate the value of parameter λ (Pagel 1999), which ranges from 0 to 1. Values of $\lambda = 0$ indicate an absence of phylogenetic signal, and values of λ close to 1 indicate that the residuals fit a Brownian Motion model of evolution. In addition to reporting the levels of phylogenetic signal based on λ for model residuals, we report phylogenetic signal for the response variables (i.e. Range filling100 and Range filling 95), to assess the extent to which the explanatory variables absorb the phylogenetic structure in the response.

Phylogenetic data

For analyses of mammals we utilized the Fritz et al. (2009) mammal super-tree, which provides an almost-complete phylogeny of mammal species. For birds, we randomly sampled 1,000 trees from the posterior distribution of the "Ericson backbone" bird phylogeny (Jetz et al. 2012) pruned to contain all initial 335 bird species in our analyses. In the latter case, we run a PGLS for each of the 1,000 trees in order to account for phylogenetic uncertainty (Bollback 2005) and thus, we report average values for model parameters (i.e. model coefficients, their standard error, and their significance) together with their 95% Confidence Intervals. We pruned the phylogenetic trees to include only targeted species, and after removing discrepancies between the trees and the databases, our PGLS analyses encompassed a total of 88 mammal species and 282 bird species.

Results

PGLS analyses identified predictor variables in the combined models for which model coefficients are no longer significant once phylogenetic relationships among species are accounted for (i.e. sleep behavior in mammals, and body mass and annual productivity in birds; see Tables S3.1 and

S3.2, respectively). We note that phylogenetic signal both in the response variables and the residuals were low, particularly in the case of mammals.

Table S3.1. Combined PGLS models for **mammals** taking into account phylogenetic relationships. β: model coefficients; SE: standard errors. Note that significant predictors at p<0.1 are indicated in bold. Units of variables are detailed in Appendix S1.

	Range filling100			Range filling95		
	β	SE	*p*	β	SE	*p*
Intercept	0.174	0.070	**0.015**	0.188	0.073	**0.012**
Habitat breadth	0.063	0.015	**0.000**	0.063	0.016	**0.000**
Allometric sexual maturity age	-0.044	0.023	**0.058**	-0.048	0.024	**0.049**
Sleep behaviour	-0.075	0.046	0.103	-0.071	0.048	0.144
λresponse	5.073E-16			8.359E-16		
λresiduals	9.437E-17			6.034E-17		

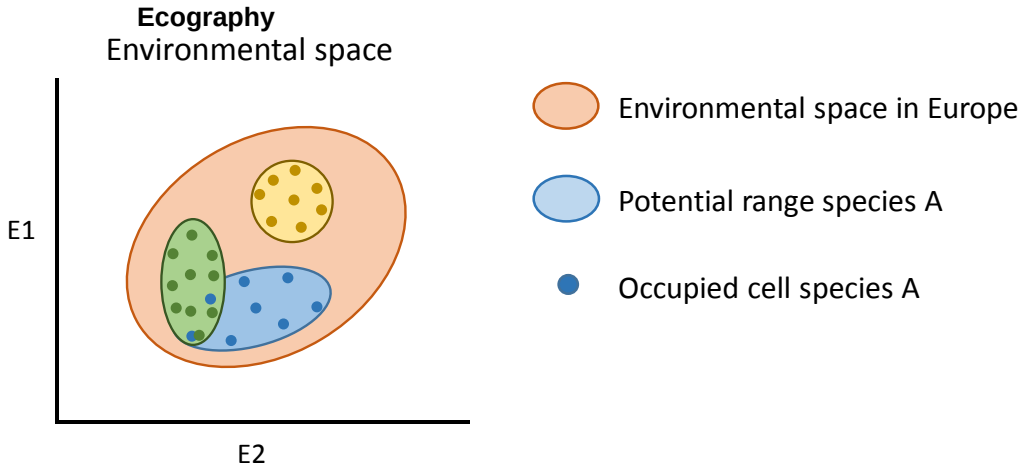
Table S3.2. Combined PGLS models for **birds** taking into account phylogenetic relationships. Since results are computed across a subset of 1,000 phylogenies from the posterior distribution of Jetz et al. (2012), both average values and upper and lower Confidence intervals are indicated for each parameter. Note that significant predictors at p<0.05 are indicated in bold. β: model-averaged coefficients; SE: standard errors averaged across models. Units of variables are detailed in Appendix S1.

	Range filling100									Range filling95								
	β	+CI	-CI	SE	+CI	-CI	*p*	+CI	-CI	β	+CI	-CI	SE	+CI	-CI	*p*	+CI	-CI
Intercept	0.095	0.098	0.093	0.121	0.122	0.120	0.431	0.445	0.417	0.109	0.111	0.107	0.127	0.128	0.126	0.392	0.405	0.378
Habitat breadth	0.032	0.032	0.032	0.010	0.010	0.010	**0.001**	**0.001**	**0.001**	0.031	0.031	0.031	0.010	0.010	0.010	**0.002**	**0.002**	**0.002**
Annual fecundity (log)	0.195	0.196	0.195	0.031	0.031	0.031	**0.000**	**0.000**	**0.000**	0.198	0.199	0.198	0.032	0.032	0.032	**0.000**	**0.000**	**0.000**
Allometric longevity	0.187	0.187	0.187	0.030	0.030	0.030	**0.000**	**0.000**	**0.000**	0.184	0.184	0.183	0.031	0.031	0.031	**0.000**	**0.000**	**0.000**
Body mass (log)	-0.012	-0.012	-0.012	0.012	0.012	0.012	0.327	0.336	0.318	-0.013	-0.012	-0.013	0.013	0.013	0.013	0.332	0.341	0.323
Annual productivity (log)	-0.007	-0.006	-0.007	0.028	0.028	0.028	0.806	0.816	0.795	-0.008	-0.008	-0.009	0.029	0.029	0.029	0.775	0.785	0.764
λresponse	0.167	0.170	0.163							0.168	0.183	0.152						
λresiduals	0.185	0.189	0.181							0.198	0.198	0.197						

Range filling

Potential range: PCA-environmental approach

Range filling (rf): proportion of the climatic potential range that it is occupied



Modelling method

Quasi-binomial GLMs

rf ~ predictive traits

Modelling steps:

1: Univariate models — rf ~ each predictive trait
- Deviance explained (DE) > 10% -- core traits
- DE < 10%, P < 0.25 -- candidate traits
- DE < 10%, P > 0.25 -- discarded traits

2: Multivariate models
- rf ~ core traits + candidate trait 1
- rf ~ core traits + candidate trait 2
- …

→ RVI > 0.5 – selected traits step 2

3: Multivariate models — rf ~ selected traits step 2
All possible combinations – Best model subset ΔQAICc <2
Remove collinear traits

4: Averaged model with the best subset of models of step 3 that excludes collinear traits – combined models

5: PGLS of combined models

6: Averaged model with significant traits in the PGLS – **Final combined models**